

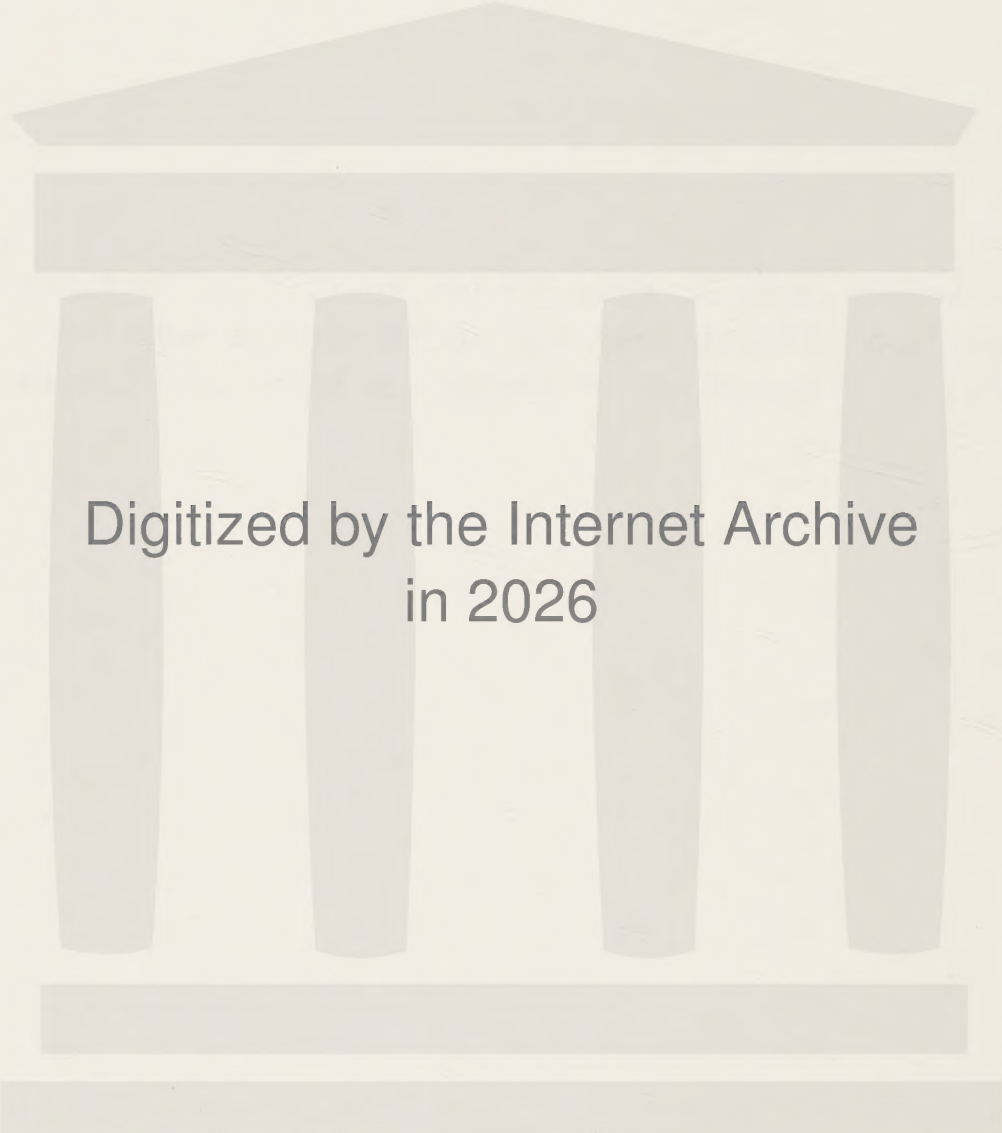
INFLUENCE OF CHEMICAL COMPOSITION,
ADDITION OF RASPBERRY LEAVES, AND
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RATE AND DYNAMIC OF NITROGEN
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LITTER

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Abstract

Newly fallen beech (Fagus silvatica L.) leaves from three forests of contrasting vegetation type in southern Sweden were incubated in pots on an identical soil under laboratory conditions. During a 26-week period at +12°C weight loss rates were similar for all three leaf types, but initially they were somewhat higher for leaves from the most fertile site. There was an absolute accumulation of nitrogen in the leaf litter, which was accelerated by supplying the element in organic or inorganic form to the soil. Nitrogen in protein added under the layer and both nitrogen and phosphorus of wild raspberry leaves mixed with it was transferred into the decomposing litter, but gave no or only a slight increase in weight loss rate. The different reactions indicated that the nitrogen availability to decomposer microbes in the litter in combination with a low lignin content resulted in increased decomposition rate. The initial nitrogen concentration seemed to influence weight loss only during the initial period of decomposition. Phosphorus was transferred into litter by similar mechanisms as nitrogen, but was retained less efficiently, indicating a non-limiting availability for decomposer activity. No accumulation in litter from nitrogen deposition in simulated rain could be noted, but a certain unexplained increased weight loss.

Finally, a discussion is given of different factors which might regulate the turn-over rate of organic matter and plant nutrients in soils of different beech forest types.

1. Introduction

Beech (*Fagus silvatica* L.) forests of contrasting vegetation types in southern Sweden are, among other things, characterized by different productivity, element concentrations in biomass and turn-over rates of litter (Nihlgård and Lindgren 1977). Field measurements in the same area (G. Petersson unpubl.) have suggested that the decomposition rate of beech leaf litter is a site-dependent variable; weight loss is rapid on sites with a vigorous field vegetation and slower on sites where the vegetation is poorly developed. At present, the factors that differentiate beech litter decomposition and their possible influence on the plant nutrient cycling of these forests are unknown.

Apart from the influence of climatic conditions, it is known that the chemical characteristics of the litter as well as those of the soil to which it is added, regulate decomposition rate (Van Cleve 1974). Results of studies in one beech forest indicate that the availability of nitrogen, and possibly also of phosphorus and sulphur, was limiting decomposer activity in leaf litter during the first one and a half years of decomposition (Staaf 1979). It also seems as if nitrogen from external sources can be transferred into the litter structure, as a considerable absolute increase of the element amounts was noted in the litter during the same period. If these indications are correct the initial nitrogen concentration of beech leaf litter should influence its weight loss rate. But it also means that other site-dependent factors, like the plant nutrient supply from throughfall and decomposing field vegetation litters, might interact with the decomposition process.

Anderson (1973) suggested that the absolute increase of nitrogen in decomposing beech leaf litter was accounted for by fungal hyphae translocation. He also concluded that incorporation of nitrogen to litter did not accelerate the decomposition rate during the first year after leaf fall.

The same phenomenon has been reported for oak leaf litter (Bocock 1963), and here precipitation, insect frass and plant material from the canopy was determined to be the most important sources of nitrogen added to litter. Gilbert and Bocock (1960) found that decomposing ash leaf litter did not accumulate nitrogen, whereas transplanted oak litter gained more nitrogen on a moder site than on a mull site. They noted no difference in weight loss between the sites for oak litter but a significant difference for ash litter. The results above indicate that both litter type and factors in the soil environment can influence the weight loss and nitrogen accumulation pattern. There is, however, incomplete knowledge about which of them is the most important in this respect.

In the present study the decomposition of leaf litter from some southern Swedish beech forest sites was followed under controlled laboratory conditions. The aim was to see whether a) weight loss and b) the nitrogen and phosphorus dynamic of the litter were influenced by any of the following factors:

- the initial chemical composition of the litter as determined from its forest type origin,
- the mixing with another litter type with higher nutrient content and higher decomposition rate,
- the addition of inorganic nitrogen in simulated rain,
- the addition of an organic nitrogen source to the soil below the litter layer.

2. Materials and methods

Newly fallen leaves of common beech were collected during the first week in November 1976 in three forests in the southernmost province of Sweden. The sites were selected to represent as large a span as possible of beech forest vegetation types existing in the area, according to Lindgren (1970), and were as follows:

Site_I_

(Kongalund) - a mature beech forest with a fully covering field layer characterized by Lamium galeobdolon L. and Stellaria nemorum L.. The sandy brown forest soil of the site has a weakly developed mull horizon with a $\text{pH}_{\text{H}_2\text{O}}$ of 5.0-5.5.

Site_II

(Nyteboda) - a mature beech forest on a stony moraine of archaean origin. The sparse field layer is dominated by Deschampsia flexuosa L. and the soil profile is a podsol with a thin mor layer ($\text{pH}_{\text{H}_2\text{O}}$ 4.5-5.0).

Site_III_

(Dalby) - a mixed deciduous forest on a calcareous clay, a luxuriant field layer; in summer dominated by Mercurialis perennis L., and with a deep mull layer of $\text{pH}_{\text{H}_2\text{O}}$ 6.5-7.0.

At each locality one composite sample of beech leaves was taken from the ground on about 25 spots in two diagonals within a 50 x 50 m plot. Wild raspberry (Rubus idaeus L.) leaves were also collected at site I. The litter was then allowed to dry at room temperature for one week. Incubations were made in 10 cm high 1 dm³ plastic pots with drainage holes and filled from the bottom with; 2 cm turf, 5 cm mull material from site I, and finally 1 cm of A₀₂ material from site I. The A₀₂ material was mainly made up of far decomposed but still indentifiable beech leaves. Five sets of pots with the following A₀₁ litters were prepared:

- a. Beech leaves (2.7 g dw/pot) from site I
- b. Beech leaves " from site II
- c. Beech leaves " from site III
- d. Beech leaves " from site I + raspberry leaves (0.9 g dw/pot).
- e. As c but with 0.4 g casein (15% N) placed between the mull and the A₀₂ horizon of each pot.

Thirty-two pots of each set were placed in a thermostat at $+12 \pm 1^{\circ}\text{C}$, watered with totally 100 ml demineralized water each during the first week, and then sealed at the top with a thin polythene foil preventing water losses but allowing gas exchange. After 6, 12, 18, and 26 weeks eight pots from each treatment were unsealed, watered with 100 ml demineralized water and allowed to drain for two days. The litter of each pot was then sorted, dried at 85°C and the remaining weight determined. Chemical analyses were performed as triple determinations on ground composite samples from the eight parallels.

In autumn 1977 beech leaves from site I were collected and incubated for 18 weeks in a fundamentally similar mode as described above. Three sets of pots, each with ten parallels were prepared; one control set of pots treated as the a-set above and two sets of unsealed pots watered with demineralized H_2O and NH_4NO_3 -solution respectively. Every second day 30 ml of water, corresponding to 2.3 mm rain, were given to each of the unsealed pots. The set with nitrogen additions was given $3.5 \text{ mg N} \cdot \text{l}^{-1}$ artificial rain, which is approximately double the concentration in throughfall in the Kongalund forest (site I) (Nihlgård 1970). The additions gave 5.6 mg N per pot in 190 mm artificial rain during 18 weeks. Temperature in the incubation room was kept at $+12 \pm 1^{\circ}\text{C}$ and relative humidity at $75 \pm 10\%$. Ten pots of each set were sampled after 6 and 18 weeks of incubation; the control set, though, only after 18 weeks. After drying, each sample of litter was individually analyzed for weight loss and total nitrogen content.

Nitrogen was determined by traditional semi-micro Kjeldahl analysis (Nihlgård 1972). Total phosphorus content was analyzed with spectrophotometry using the yellow-vanadate-phosphate complex method (Jackson 1958) and potassium with flame photometry after a wet oxidation of samples in concentrated $\text{HNO}_3 + \text{HClO}_4$ (Johnson and Ulrich 1960).

Sulphur was analyzed as Ba SO_4 with a turbidometric method (Blanchard et al. 1965) after wet oxidation as above. The amount of water-soluble and acetone-soluble substances were determined by sonicating the milled samples for three consecutive times in a sonicator bath and weighing the samples after filtration and drying. Lignin was analyzed gravimetrically as Klason lignin according to Bethge et al. (1971).

3. Results and discussion

3.1 Influence of initial chemical composition of the litter

In spite of the fact that the beech leaves originated from sites of very different forest and soil type their chemical composition was rather similar (Table 1), as also reflected by the weight loss results (Table 2). Only during the first half of the decomposition period did leaves from a site, in this case site III, differ slightly but statistically significant from the others in this respect. Their higher weight loss can not be explained by a higher availability of either nitrogen or phosphorus if total concentrations of these elements in litter are considered to be an index of this availability. In fact, the initial nitrogen content of site I leaves was considerably higher than the others without any obvious effect on decomposition rate. On the other hand, site I leaves had the highest content of lignin, a substance which has been found to reduce decomposition rate in litter (Van Cleve 1974, Fogel and Cromack 1977), which might have counteracted such a positive tendency. If so, the lower initial lignin content in leaves from site III can explain the obtained weight loss differences, which result from the opposing influence of increased nitrogen and lignin contents of the litter.

Judging from the increasing nitrogen and phosphorus concentrations (Fig. 1), both elements were retained in the litter as

related to the total weight loss. For nitrogen there was also an absolute increase in total amounts in all three litter types, while there was a continuous but slow net loss of phosphorus. The rate of phosphorus loss tended to be positively related to the initial total concentration of the element. In the period 18-26 weeks the concentrations of both elements became nearly constant, and there was an absolute decrease of nitrogen in leaves from sites I and III, but not in those from site II.

The results show that nitrogen and, at least during one period, also phosphorus were imported to the leaf litter/decomposer structure. A supply of these elements by wet or dry deposition was excluded by the experimental conditions. Moreover, a similar experiment performed by Remachle and Vanderhoven (1973) had earlier demonstrated that nitrogen fixation does not influence the nitrogen content of decomposing beech leaf litter. This makes nitrogen and phosphorus in old litter or humus below the incubated leaves the most possible source, and a transfer by means of fungal hyphae the most probable mechanism for the import. For decomposing needle litter a positive relation between nitrogen accumulation and the amount of ingrowing fungal hyphae has been reported (Berg and Söderström 1979), and in the present case a marked increase of visible hyphae bundles was noted after 18 weeks of incubation.

To be able to interpret what determines the element dynamics in the litter some assumptions must be made on it is utilized by decomposers. The general idea is here that different organic compounds are broken down to furnish decomposers with energy and nutrients. A high availability of organic carbon will thus give a high potential for microbial production and thereby decomposition rate, since carbon constitutes about half the weight of organics used for respiration and tissue build-up. This potential is determined by the structural and chemical quality of the litter, and can only be utilized as far as is permitted by the availability of other nutrients like nitrogen and phosphorus, as well as temperature and moisture conditions.

It is further assumed that the nutrient elements are primarily supplied from the decomposed substrate , but is transferred by decomposers from sources outside the litter when the availability within it becomes suboptimal. The latter statement is applicable only to hyphae-forming fungi. A final necessary pre-assumption is also that mineralized nutrients are water-soluble and not to any significant degree retained in litter by abiotic processes. The latter statement seems reasonable to apply to the present investigation, which implies that there is a close relationship between net mineralization of nitrogen and phosphorus and the observed loss rates from litter.

It appears from this general view that both nitrogen and phosphorus concentrations in the beech leaf litters used here were suboptimal for microbial decomposition, as these elements were retained or even imported to them. Nitrogen- and phosphorus-rich compounds in the litter must have been decomposed earlier in leaves from site III than in the others, since the weight loss of the former was highest in spite of a lower total concentration than in e.g. those of site I. The nitrogen input to leaves from site I already during the first six weeks, on the other hand , indicates that the nitrogen availability was lowest in this litter type, possibly an effect of its high lignin content. A decrease in the nitrogen concentration (Fig. 1) in site I leaves after 18 weeks was coupled with a tendency to a retarded weight loss rate (Table 1). This might be seen as an indication of an increased resistance of the organic compounds to decomposition, making the nitrogen demand of decomposers lower and allowing a net loss of the element to occur.

3.2. Influence of organic and inorganic nutrient additions

3.2.1. Addition of raspberry leaves

Raspberry leaves differed in chemical composition from those of beech; a higher potassium concentration, a larger water-

-soluble fraction and a lower lignin content being the most obvious differences (Table 1). The weight loss pattern was also fundamentally different to that of beech leaves (Fig.2). Mixing of these two litter types caused the concentrations of nitrogen and phosphorus in beech litter to increase during decomposition (Fig.3), but no change in weight loss could be noted (Table 2).

The net accumulation of elements in beech leaves started earlier for phosphorus than for nitrogen. It can not be explained by a direct transfer from the raspberry leaves during the 6th to the 12th week, since the phosphorus loss from these was very small during this period (Fig. 4). Between the 12th and the 18th week, however, such a transfer seems plausible for nitrogen and for half of the phosphorus increase. A transfer by ingrowing hyphae is here a probable mechanism because of the simultaneous and quantitatively equivalent import of the two elements to litter.

A general feature of these results is that both nitrogen and phosphorus in added raspberry leaves were transferred to decomposing beech leaves. Amounts and concentrations of elements increased but did not change the basic trends in element changes or in decomposition rate. Furthermore, the additional element accumulation in beech leaves was not fully synchronized with the net loss from raspberry leaves, especially for phosphorus. Consequently, the release of nitrogen and phosphorus from sources outside the litter structure only slightly influenced the accumulation of these elements in it. Thus, the import of elements was probably not a passive physical process, but instead regulated by the decomposition pattern of the litter. If this is correct it means that, under prevailing conditions, the availability of nitrogen for decomposer microorganisms with ability to use nutrient sources outside the beech leaf litter was optimal, without any additional supply.

3.2.2. Protein addition

Addition of protein under the litter, corresponding to about double the amount of nitrogen in the investigated beech leaves of each pot, caused an enhanced accumulation of nitrogen in litter. It did not influence the phosphorus dynamic of it (Fig. 3), but a slight positive effect on weight loss was noted after 12 weeks of incubation (Table 2). The nitrogen import mainly occurred during the initial six weeks, which made a fundamental difference to the change of elements induced by the addition of raspberry leaves. In the later parts of the study period the relative changes in remaining amounts of the elements were unaltered (Fig. 3), but the nitrogen concentration in litter remained at a level 15-20% higher than normal.

Since casein is insoluble at a pH of about 5, which is prevailing in the litter layer, it must have been decomposed to water-soluble products and then transferred through the A_{02} litter horizon. In light of the earlier statements on nitrogen import to litter it seems reasonable to assume that the rapid initial nitrogen accumulation was an effect of a passive transport. This supply might have stimulated the activity of decomposer organisms without the ability of an active import to the substrate litter, e.g. bacteria, causing the increased decomposition rate. This would explain the difference to the reaction following an addition of raspberry leaves. The active import of nitrogen supplied from these leaves did not significantly alter the accumulation pattern in litter. Assuming that there was a supply of organic nitrogen, amino acids in this case, which also would have served as an energy source, the suggested mechanism for the stimulating effect on decomposition is still more plausible.

3.2.3. Wet deposition of nitrogen

The amount of nitrogen added to the fertilized experimental set was of the same magnitude as in throughfall of the Konga-

lund forest (site I) during a vegetation period (Nihlgård 1970, Nilsson 1978), but presented in a smaller amount of water. This made the leaves drier than those in the sealed pots and the decomposition rate lower (Table 3), but probably produced more realistic vertical water movements through the litter in relation to the field situation.

No significant differences between the sets were found after the first 6 weeks of decomposition. A slight but significantly ($0.01 > p > 0.001$) higher weight loss could be noted after 18 weeks as an effect of the nitrogen additions in simulated rain (Table 3), but it was not coupled to any nitrogen concentration increase in the litter. Judging from the very small differences in remaining amount of nitrogen on both sampling occasions it appears reasonable to conclude that the added amount was not an important source of the accumulation of this element in litter. These results confirm the earlier statements about the weak influence of additional supplies to external nitrogen sources on their transfer to litter. However, its effect on weight loss still remains to be satisfactory explained.

4. Conclusions and field applications

Beech leaf litter from three very different forest types displayed uniform decomposition rate when incubated under identical environmental conditions. An initially higher weight loss of leaves from the most fertile site as interpreted as an effect of a lower lignin content compared to the others, in combination with a higher nitrogen concentration. Both nitrogen and phosphorus availability seemed to be initially suboptimal for decomposition. However, considerable amounts of nitrogen were imported to the litter during the incubation period and differences in phosphorus concentrations were quickly levelled out, and these elements are not likely to differentiate decomposition rates of these litters in the long run. From this it appears that litter quality does not determine the different

turn-over rates of litter found in beech forests of southern Sweden (c.f. Nihlgård and Lindgren 1977). Leaves constitutes the dominant litter fall components of these forests.

Environmental factors might be expected to regulate both specific rates of, and the potential for, litter disintegration. The latter comprises species and biomass structure of decomposers, which are too sparsely known among the discussed beech forests for us to be able to conclude how it might contribute to the site-dependent variation in decomposition rate. Effects of chemical litter factors on decomposition and fragmentation by soil animals is not considered in the present experiments, since the litters were incubated on a soil with a low macro-fauna population. Another biotic factor of importance might be the retarding influence on mycorrhiza upon litter decomposition, which has been found to exist in forests of Pinus radiata (Gadgil and Gadgil 1975). The action of such a factor here is purely hypothetical, but Björkman (1942) found that the mycorrhiza frequency decreased with an increasing soil fertility of beech forests in southern Sweden.

Climatic factors like temperature and moisture are also known to influence the weight loss rate of litter (Witkamp 1966). The macro-climate is fairly similar within the discussed beech forest area in Sweden, but the relief of the landscape and the very different soil textures make the soil moisture conditions highly variable. In the present investigation the soil moisture regime greatly influenced the decomposition rate and is likely to do so also in the field.

Beech forests also have a great inter-site variation in ground vegetation. The additions of leaves of wild raspberry, a plant which is common in mature forests on fertile sites, produced conditions for a transfer of both nitrogen and phosphorus to the beech leaf litter. Plant nutrients

added from other litter types, from rainfall or from other sources in the soil gave no or only a very slight enhancement of litter decomposition. Thus, the existence of a "priming effect" of herb and shrub litter on the mineralization of carbon, nitrogen or phosphorus from tree litter in beech forests must be doubted, at least during the initial period of decomposition. The transfer of plant nutrients, however, is likely to level out release rates from litter layers of a mixed plant species and structural origin. Such a mechanism might be of importance in reducing losses from the ecosystem of the essential plant nutrients that are liberated from rapidly decomposing nutrient-rich field vegetation litter.

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Table 1. Some chemical properties of the litter used in the incubations and collected in the autumns of 1976 and 1977.

Locality	Year of collection	Litter type	Total			concentration (mg g dw ⁻¹)	of:	lignin
			N	P	K	S		
Site I	1977	beech leaves	8.5	n.d.	n.d.	n.d.	n.d.	n.d.
	1976	beech leaves	11.2	0.83	1.8	1.4	50	440
	1976	raspberry leaves	14.1	0.81	10.9	n.d.	253	178
Site II	1976	beech leaves	8.4	0.93	2.0	1.1	53	400
Site III	1976	beech leaves	9.5	0.78	1.9	1.3	57	380

n.d. = not determined

Table 2. Weight loss of beech and raspberry leaves after different periods of incubation. The significance levels of the difference¹⁾, according to t-tests, to values for beech leaves from site I are also given. Samples from autumn 1976.
CL means confidence limits. N=8.

Litter type	W e i g h t	L o s s (% of initial weight)	a f t e r:
	6 weeks	12 weeks	18 weeks
	$\bar{x} \pm 95\%CL$	$\bar{x} \pm 95\%CL$	$\bar{x} \pm 95\%CL$
Site I			
a, beech leaves	5.7±1.2	11.8±1.6	19.5±1.6
b, beech leaves, protein added	7.0±1.5	13.6±0.9 *	19.5±1.1
c, beech leaves, raspberry leaves added	5.1±1.3	11.8±1.4	18.7±2.0
d, raspberry leaves	23.0±4.0 ***	41.2±7.1 ***	62.0±6.4 ***
Site II			
beech leaves	6.1±1.1	11.7±1.6	19.7±1.0
Site III			
beech leaves	7.8±1.6 *	14.5±1.1 **	21.2±2.1
			27.7±3.9

1) * = 0.05>p>0.01, ** = 0.01>p>0.001, *** = p<0.001

Table 3. Weight loss, nitrogen concentration and nitrogen amount in beech leaves, variously treated, - from site I after 6 and 12 weeks of incubation in the laboratory. Mean figures of ten replicates are given together with 95% confidence limits. The litter was collected in autumn 1977.

	Weight loss			Nitrogen concentration			Remaining amount of nitrogen		
	(% of initial amount)			(mg g dw ⁻¹)			(% of initial amount)		
Incubation time (weeks)	0	6	18	0	6	18	0	6	18
1. Sealed pots	0	n.d.	14.2	8.5	n.d.	11.4	100	n.d.	115
			±0.5			±0.4			± 4
2. Unsealed pots									
a. watered with demineralized H ₂ O	0	5.6	9.8	8.5	9.4	10.8	100	105	114
		±0.5	±0.5		±0.4	±0.2		± 3	± 3
b. watered with NH ₄ NO ₃ -solution	0	5.2	10.9	8.5	9.2	11.0	100	103	115
		±0.6	±0.3		±0.1	±0.2		± 1	± 2

n.d. = not determined

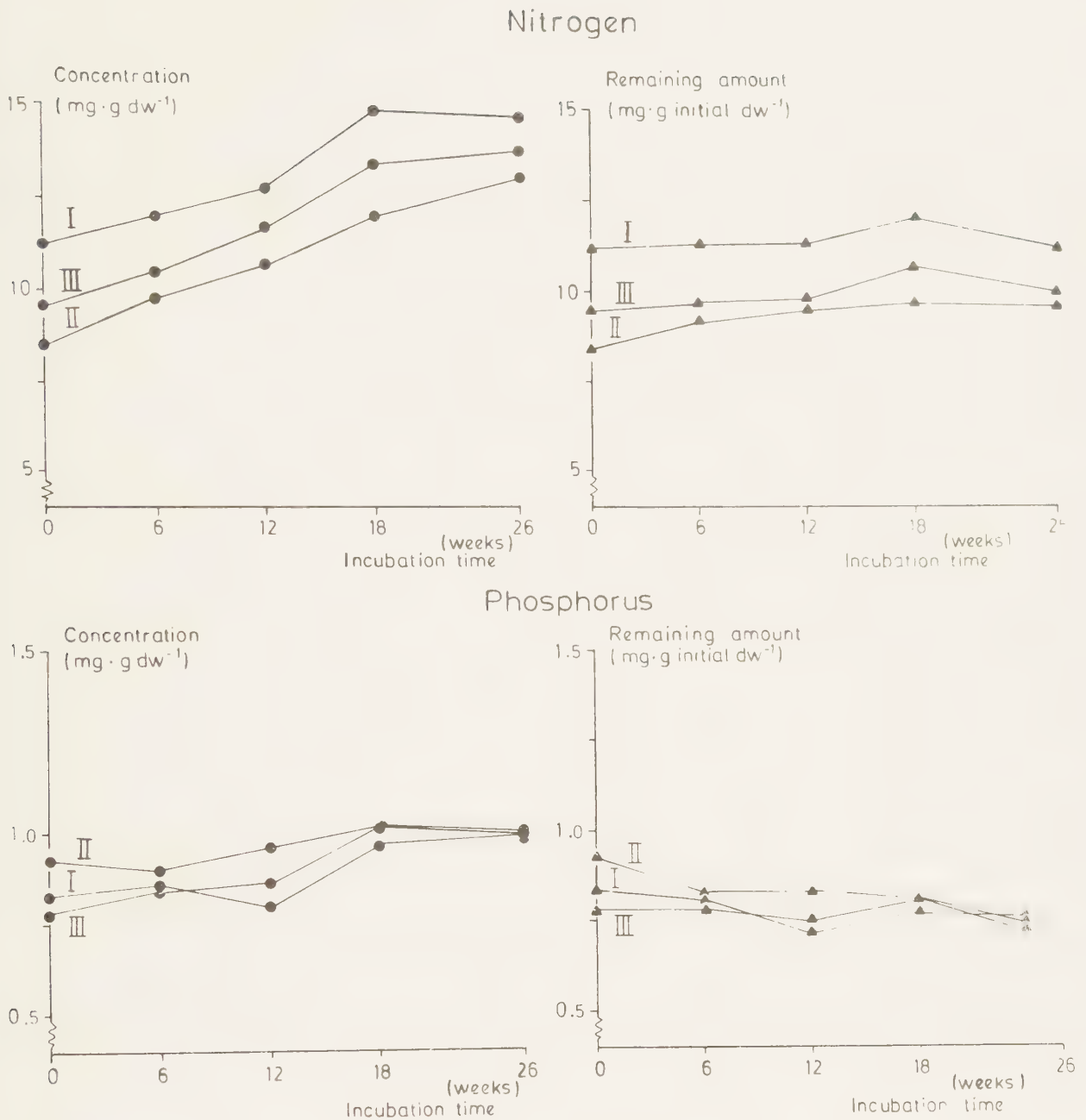


Figure 1. Changes in concentrations and amounts of nitrogen and phosphorus in decomposing beech leaf litter from site I (I), site II (II), and site III (III). The leaves were collected in the autumn of 1976.



Figure 2. Remaining amount of 1 g dw of beech and raspberry leaf litter from site I after different periods of incubation.

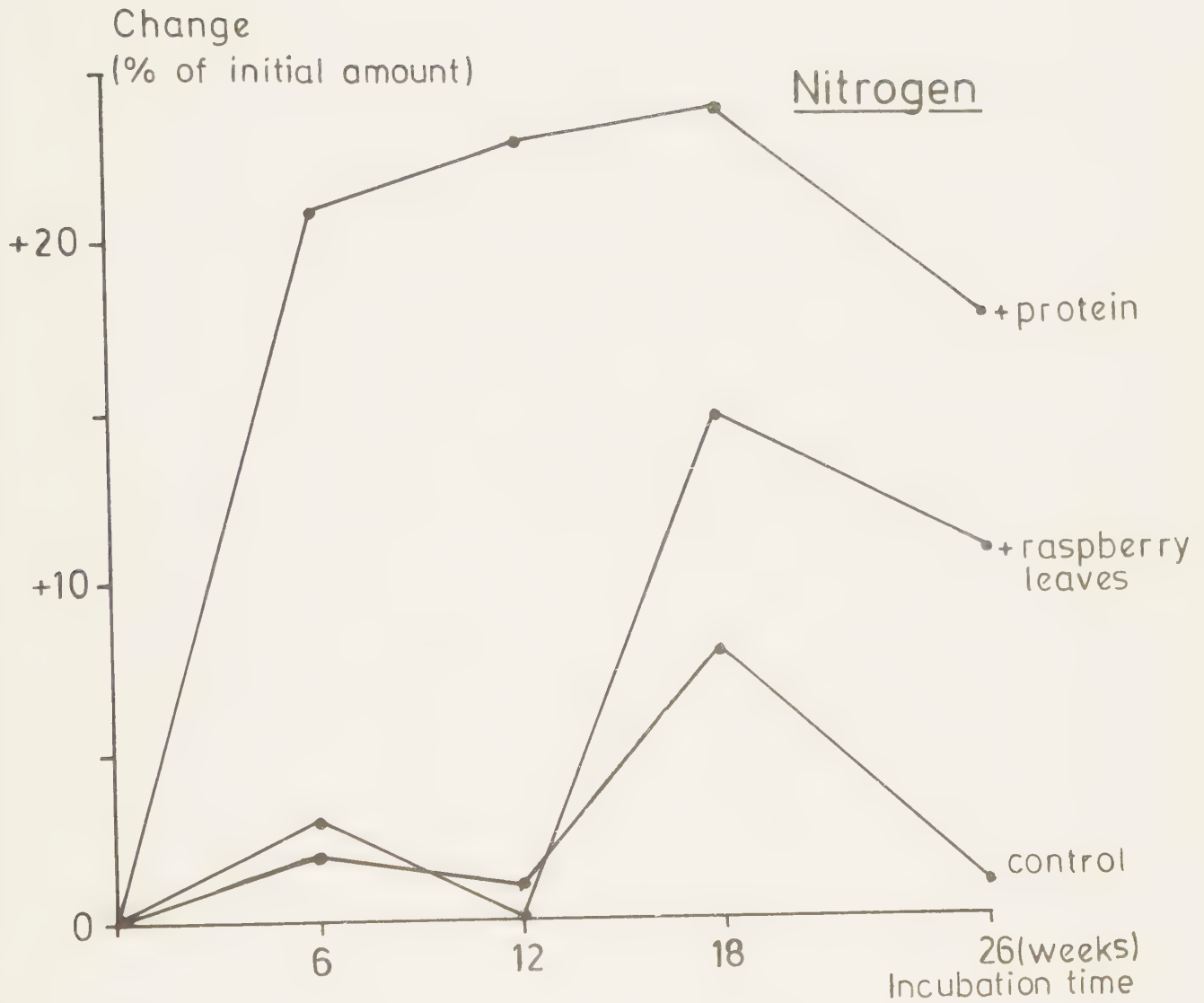


Figure 3. Changes in amounts of nitrogen and phosphorus, in relation to initial contents, of decomposing beech leaf litter (control), beech leaf litter with added protein (+protein), and beech leaf litter with added raspberry leaves (+ raspberry leaves). The leaves were collected at site I in the autumn of 1976.

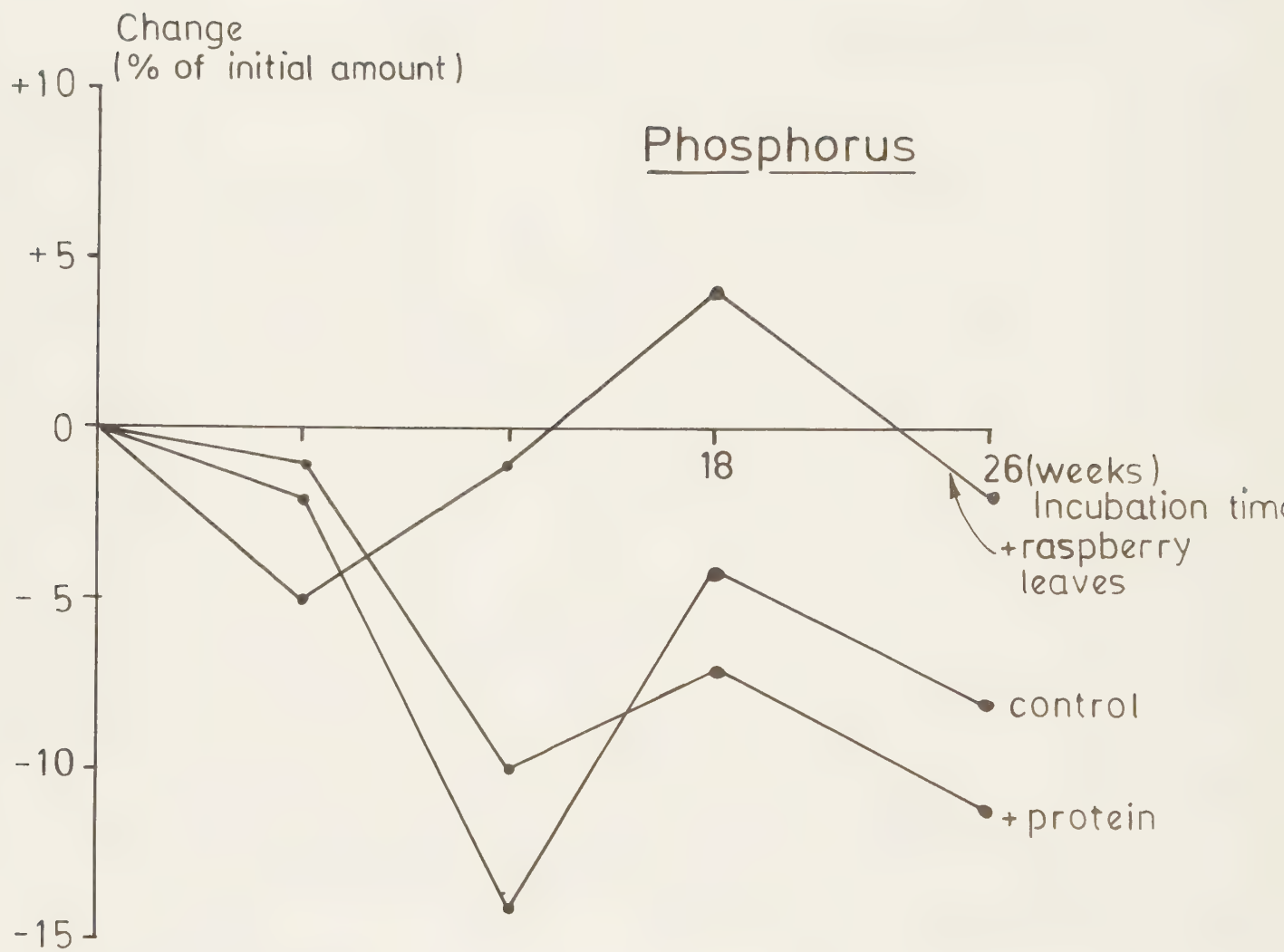


Figure 3. (Continued)

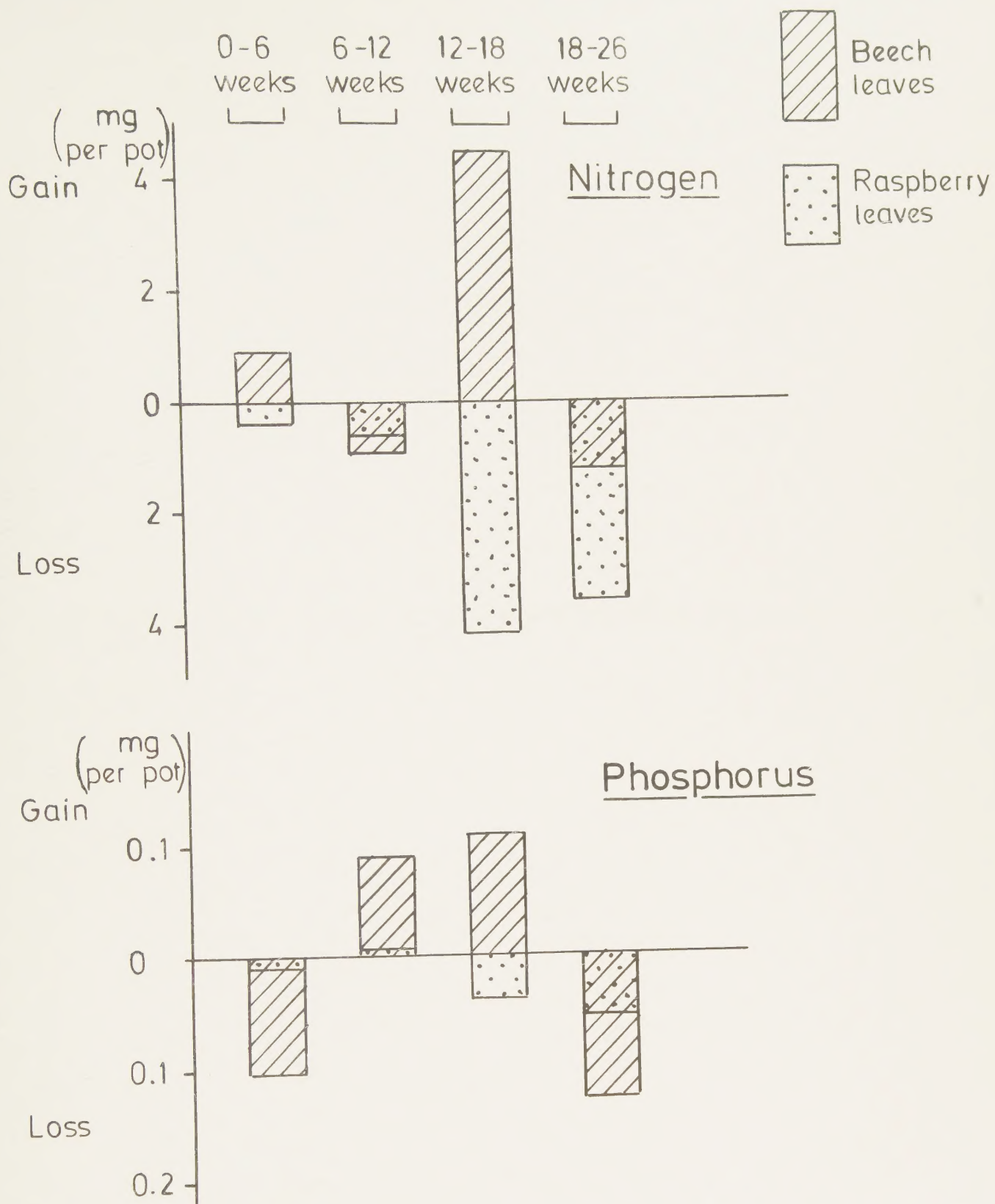


Figure 4. Changes in absolute amounts of nitrogen and phosphorus in mixed beech leaf litter (2.7 g dw per pot) and raspberry leaf litter (0.9 g dw per pot) during different incubation periods. The leaves were collected in the autumn of 1976 at site I.

